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ECOLOGY OF THE EUROPEAN WILD RABBIT, *ORYCTOLAGUS CUNICULUS* (L.), IN MEDITERRANEAN HABITATS

I. DISTRIBUTION IN THE LANDSCAPE OF THE COTO DOÑANA, S. SPAIN

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SUMMARY

(1) The distribution pattern of the European wild rabbit in the Reserva Biológica de Doñana is described in relation to an objective landscape analysis of the study area.

(2) The landscape consists of three principal sand dune land systems, the youngest of which is still forming, lying between the Atlantic Ocean and the alluvial deltaic plain of the Río Guadalquivir, Las Marismas. The climate is one of hot dry summers and mild wet winters. Las Marismas and smaller border areas of the sandy land systems form seasonal marshes each winter.

(3) Rabbits are distributed discontinuously and are concentrated near moist grassland areas near borders of land systems.

(4) Detailed distribution patterns in apparently favourable and unfavourable areas showed that rabbits thrive best where sand ridges suitable for warren building interdigitate or abut moist feeding grounds.

(5) It is suggested that the dynamics of distribution and numbers superimposed on objective landscape analysis allows sensible wildlife management decisions to be taken in the absence of more detailed parametric study.

INTRODUCTION

The rabbit *Oryctolagus cuniculus* (L.) is of west mediterranean origin and, according to Zeuner (1963), was discovered in the Iberian peninsula by the Phoenicians in about 5000 B.C. Through natural dispersal and modern introductions it is now found worldwide (Thompson & Worden 1956). The ecology of the rabbit in mediterranean habitats is of intrinsic importance in understanding its present status as a colonist of new habitats.

Changes in population distribution patterns in relation to habitat reflect the outcome of ecological processes affecting reproduction and survival, factors fundamental to the ecology of a species. Rabbit populations in different climatic regions are distributed discontinuously, and patterns of distribution bear a direct relationship to landscape features. Myers & Parker (1975a) showed that the dynamics of distribution of rabbit populations in an arid habitat in Australia were significantly related to changes in climate and landscape. In Great Britain Lloyd (1970) referred to significant changes in rabbit distribution since myxomatosis. In this paper we describe patterns of distribution of the rabbit in a mediterranean habitat in southern Spain.

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The study region comprised a series of coastal land systems between the Atlantic Ocean and Las Marismas, the deltaic flood plains of the Río Guadalquivir. The Reserva Biológica de Doñana (6800 ha), part of the Coto Doñana, an ancient hunting reserve on which this study was centred, is representative of the region (Rogers & Myers unpublished) and forms part of the Parque Nacional de Doñana (35 000 ha).

The climate is typically Mediterranean, with hot dry summers and mild wet winters. Mean annual rainfall is 591 mm, mainly in winter, and mean temperatures range from 5 °C in January to 35 °C in July/August (40-year averages for Sevilla, Servicio Meteorológico Nacional, Sevilla).

The extremes of climate are reflected in the landscape. During winter Las Marismas become completely flooded. In spring the waters recede and vigorous plant growth ensues. In summer Las Marismas dry, leaving vast hard-baked alluvial flats covered with dead vegetation. That part of the Coto Doñana lying in the wedge of land between Las Marismas and the coastline supports a sparse xerophytic chaparral vegetation in sandy soil. The most recent dune systems have almost no permanent vegetation, though moist hollows between them may support luxuriant plant growth (Rogers & Myers unpublished). Although not pristine (Garcia 1977), the lands of the Parque Nacional are undeveloped and subject to very little agriculture or pastoralism, and therefore represent a relatively undisturbed landscape.

The area was mapped according to the landscape approach (Mabbutt 1968). The method, reviewed by Rogers & Myers (in press) involves recognition of recurrent landscape patterns on aerial photographs. A given pattern is referred to as a land system. The components of the pattern are called land facets. A land facet consists of one or more land elements (the simplest part of the landscape, for practical purposes uniform in lithology, form, soil and vegetation) grouped for convenience. This terminology follows Brink *et al.* (1966). The Reserva Biológica de Doñana includes parts of five land systems. Las Marismas land system (L.S.) is a seasonal marshland of deltaic origin. The remaining land systems (El Matorral, low heathland; Las Naves, high heathland; Dunas Bajas, low blown-out dunes; Dunas Movedizas, mobile dunes) are sand dune systems oriented similarly by the prevailing southwest wind and are described in detail by Allier, González & Ramirez 1974 and Rogers & Myers (unpublished).

The juxtaposition of land systems gives rise to zones of grassland on the east border of El Matorral L.S. and in parts of Dunas Bajas L.S. Limited grassland occurs elsewhere, mainly in El Matorral L.S. The sward of the grassland is thin and, particularly in the later months of the summer, heavily trampled. Species composition, dominated by forbs, is indicative of overgrazing (Rogers 1974). Authorities for plant names follow Tutin *et al.* (1964–76) for dicotyledons and Galiano & Cabezudo (1976) for monocotyledons.

MATERIALS AND METHODS

The distribution of rabbits in the Reserva Biológica de Doñana was measured along transects by counting animals and sampling their signs (faecal pellets, scratches, warrens). Two study plots, representing high and low densities of rabbits, and named for convenience Sanguijuela and El Muerto respectively, were examined in greater detail.

Transects (Fig. 1) totalling 30 km were selected to give representative coverage of the land systems of the reserve. Observations were made in two seasons in 1973. Following the spring flush of vegetation, live animals were counted from 30 March to 21 May and signs were sampled from 30 March to 29 April. In late summer, following the hot dry

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season and before the autumn rains, counts of live animals were made from 25 August to 26 September and sign sampled from 14 September to 5 October.

The counts of live animals were made daily from a horse during the last 2·5 h before sunset. Transects were ridden in rotation, three times in each direction. Counts of animals were converted to indices of density by Hayne's (1949) method (Giles, 1969) as follows:

$$\text{Density} = \frac{C}{2L}\sum \frac{n_i}{d_i} \text{ animals/unit area}$$

where L = length of transect in a given landscape unit; n_i = number of animals in ith observation; d_i = distance from observer to animal or centre of group of ith observation; C = constant for units. The distance d_i was judged by eye, after practice with marked objects at measured distances.

Rabbit sign was sampled at five random 50m radius circles per land facet on each transect. Each circle was searched from a horse for warrens, noting the total number of entrances to each and the number active. Total faecal pellets and scratches were counted and presence or absence of tracks noted in ten random 1 m² quadrats per circle.

The two intensive study areas (Fig. 1), each 300 × 600 m, were marked on airphotograph enlargements of scale 1:2000 for detailed landscape analysis. Each lay along one of the transects and was relatively free of human disturbance. Land elements were marked on overlays on the photographs and checked on the ground.

In each land element, total numbers of pellets and scratches were counted in twenty random sets, each of three 1 m² quadrats. The whole area was also covered on horseback and the location of all warrens and rabbit holes marked on an overlay of the airphotograph, noting total numbers of entrances per warren and the number active. In

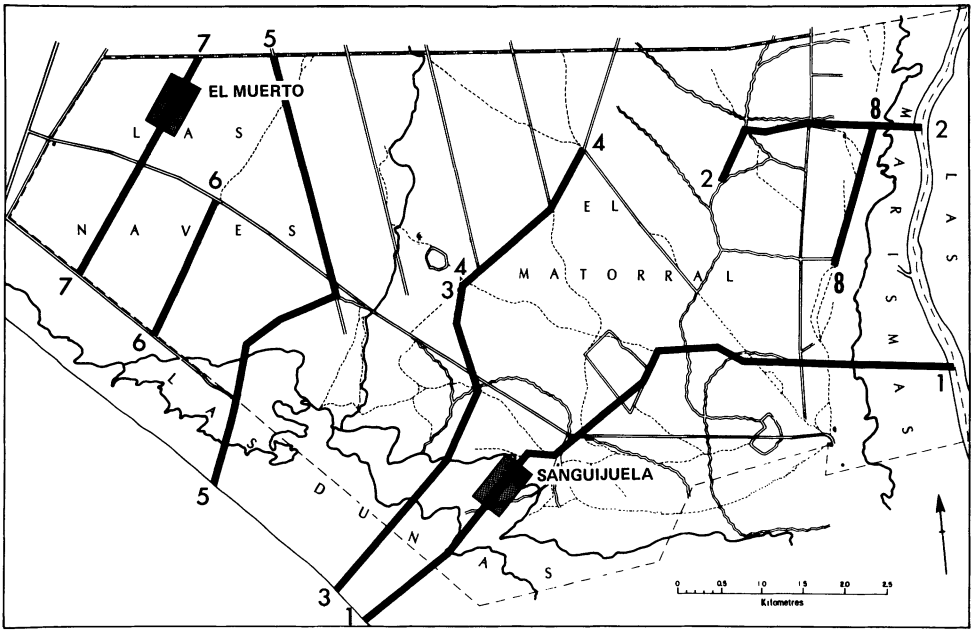


FIG. 1. Locations of transects (numbered) and the Sanguijuela and El Muerto study plots in the Reserva Biológica de Doñana.

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Sanguijuela, bushes or thickets regularly used by rabbits for shelter (hereafter called bush warrens) were also mapped on an overlay. There were no bush warrens in El Muerto.

The above observations, except mapping of bush warrens, were made once in late spring during the period of pasture growth and once in early autumn before the rains which broke the summer drought. The quadrats were marked by numbered pegs in the spring to enable identical quadrats to be inspected in the autumn. Warrens and burrows were similarly marked and numbered on both occasions. The data were subjected to two-way analyses of variance and Scheffé's multiple range test (Snedecor & Cochran 1967).

RESULTS

Regional distribution patterns in the reserve

The transect counts of rabbits showed highly significant differences between the densities of animals in different land systems. Dunas Bajas L.S. had the highest density index and El Matorral L.S. the next highest. These results were supported by the sample counts of scratches, faecal pellets, track and warrens (Table 1). In the drier systems, particularly Las Naves L.S., where rabbits were present, there was a higher incidence of scratches. Both scratches and faecal pellets tended to increase over summer as there was little disappearance of them in that season. Direct counts of animals, however, significantly decreased in numbers during summer, particularly in Dunas Bajas L.S. The number of active warren entrances also decreased in keeping with this trend. Although no data on breeding were collected, observations showed the rabbit's principal breeding period was from early spring to early summer. The above data reflect this pattern of breeding.

Analysis of the data on a larger scale (land facets) indicated that within the land systems with most rabbits, certain facets were much more important than others (Table 2). Thus in Dunas Bajas L.S. the deflation flats facet (see below) significantly more animals and signs, particularly faeces and active warren entrances, were counted. Similarly in El Matorral L.S. most faecal counts and active entrances were in the high and low facets in spring, and in the low and border facets in autumn.

Thus the deflation flats of Dunas Bajas L.S. and the low facet of El Matorral L.S. close to Las Marismas L.S. were preferred habitats in both spring and autumn. The data also suggest that in autumn there was movement of animals from more central areas to the border facet of El Matorral L.S.

Detailed patterns of distribution

Sanguijuela study plot

The Sanguijuela study plot was in the Dunas Bajas L.S., with a small part in El Matorral L.S. (Fig. 1). The former includes two facets, bare sand and deflation flats. The sand facet was not further subdivided but within the deflation flats facet three elements were recognized. They were easily identifiable on the airphotograph enlargements and were defined principally by hydrology and morphology. Those land elements of Dunas Bajas and El Matorral which occurred in the study area are described as follows (Fig. 2):

Element 1. Mobile dunes, 4–10 m high, almost devoid of plant cover except for clumps of *Corema album.*

Element 2. Sandy ridges, about 1 m high, not subject to inundation. Many bare patches, otherwise sparse plant cover (*Holoschoenus vulgaris*, *Cistus* sp., *Armeria* sp.,

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TABLE 1. Relationship between indices of rabbit numbers, land systems and seasons

	Mean transect counts: Rabbits		No. of obs. (*n*)		Mean counts of sign: Scratches[1]		Faecal[1] pellets		Track[2]		Warrens[3]		Total[3] entrances		Active[3] entrances		No. of obs. (*n*)	
	S	A	S	A	S	A	S	A	S	A	S	A	S	A	S	A	S	A
Dunas Movedizas	0·7	0·4	18	18	0·0	0·0	3·2	13·9	0·12	0·16	0·0	0·0	0·0	0·0	0·0	0·0	25	25
Dunas Bajas	95·8	42·9	18	18	0·60	1·14	138·7	361·3	0·0	0·05	1·10	1·24	4·30	6·19	2·40	0·33	20	21
Las Naves	10·2	17·5	12	12	1·59	2·27	16·5	44·5	0·04	0·10	0·31	0·67	0·90	1·97	0·21	0·0	29	30
El Matorral	34·1	37·8	24	24	0·73	1·03	31·6	149·6	0·0	0·03	0·35	1·19	1·35	3·04	0·58	0·35	74	72
Las Marismas	0·0	0·0	24	24	0·0	0·0	0·0	0·6	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	5	5

Significance of difference between means (analysis of variance)

between systems	$P <$	0·0005	0·0005	0·0005	0·1	0·0005	0·0005	0·0005
	F	50·1	20·0	40·2	2·31	13·8	14·0	9·90
between seasons	$P <$	0·5	0·1	0·0005	0·25	0·001	0·005	0·025
	F	0·13	2·90	60·5	2·38	11·5	10·4	6·48
inter-actions	$P <$	0·9	0·9	0·25	0·999	0·25	0·25	0·05
	F	0·24	0·38	1·74	0·05	1·77	1·42	2·40

[1] Number per 10 m². [2] Score out of 10. [3] Number per 50 m radius. S = spring, A = Autumn.

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TABLE 2. Relationships between indices of rabbit numbers, land facets and seasons

Land System	Land facet	Mean transect counts: Rabbits S	Rabbits A	No. of obs. (*n*) S	No. of obs. (*n*) A	Mean counts of sign: Scratches[1] S	Scratches[1] A	Faecal[1] pellets S	Faecal[1] pellets A	Track[2] S	Track[2] A	Warrens[3] S	Warrens[3] A	Total[3] entrances S	Total[3] entrances A	Active[3] entrances S	Active[3] entrances A	No. of obs. (*n*) S	No. of obs. (*n*) A
Dunas	Mobile sand	0·9	0·5	18	18	0·0	0·0	0·3	5·9	0·20	0·27	0·0	0·0	0·0	0·0	0·0	0·0	15	15
Movedizas	Depressions	0·0	0·0	18	18	0·0	0·0	7·5	26·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	10	10
Dunas	Sand	0·0	0·0	12	12	0·0	0·0	0·0	17·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	1	1
Bajas	Colonized sand	1·6	2·9	18	18	1·25	0·80	13·3	31·0	0·0	0·20	0·25	0·20	0·75	0·20	0·0	0·0	4	5
	Deflation flats	152·5	63·8	12	12	0·47	1·33	181·3	494·4	0·0	0·0	1·40	1·67	5·53	8·60	3·20	0·47	15	15
Las Naves	High	10·1	20·0	12	12	1·41	2·58	14·8	38·2	0·0	0·05	0·41	0·90	1·24	2·63	0·29	0·0	17	19
	Low	24·6	43·5	12	12	1·83	1·73	18·9	55·5	0·08	0·18	0·17	0·27	0·42	0·82	0·08	0·0	12	11
El Matorral	High	13·6	7·1	18	18	1·44	1·41	38·4	75·0	0·0	0·06	0·83	1·65	3·22	4·59	1·28	0·18	18	17
	Low	46·6	57·9	24	24	0·65	1·18	37·9	190·0	0·0	0·0	0·29	1·06	1·03	2·67	0·56	0·39	34	33
	Border	18·3	21·9	24	24	0·27	0·50	16·5	146·6	0·0	0·05	0·05	1·05	0·32	2·41	0·05	0·41	22	22
Las Marismas		0·0	0·0	12	12	0·0	0·0	0·0	0·6	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	5	5
Significance of difference between means (analysis of variance)																			
Between land facets	$P<$	0·0005				0·0005		0·0005		0·005		0·0005		0·0005		0·0005			
	F	22·5				10·1		39·5		2·55		11·5		13·4		7·99			
Between seasons	$P<$	0·5				0·1		0·0005		0·25		0·0005		0·0005		0·005			
	F	1·22				3·84		140·0		2·22		19·8		13·1		10·1			
Interactions	$P<$	0·75				0·99		0·0005		0·99		0·25		0·75		0·0005			
	F	0·72				0·29		4·63		0·27		1·35		0·83		3·83			

[1] Number per 10 m². [2] Score out of 10. [3] Number per 50 m radius circle. S = spring, A = autumn.

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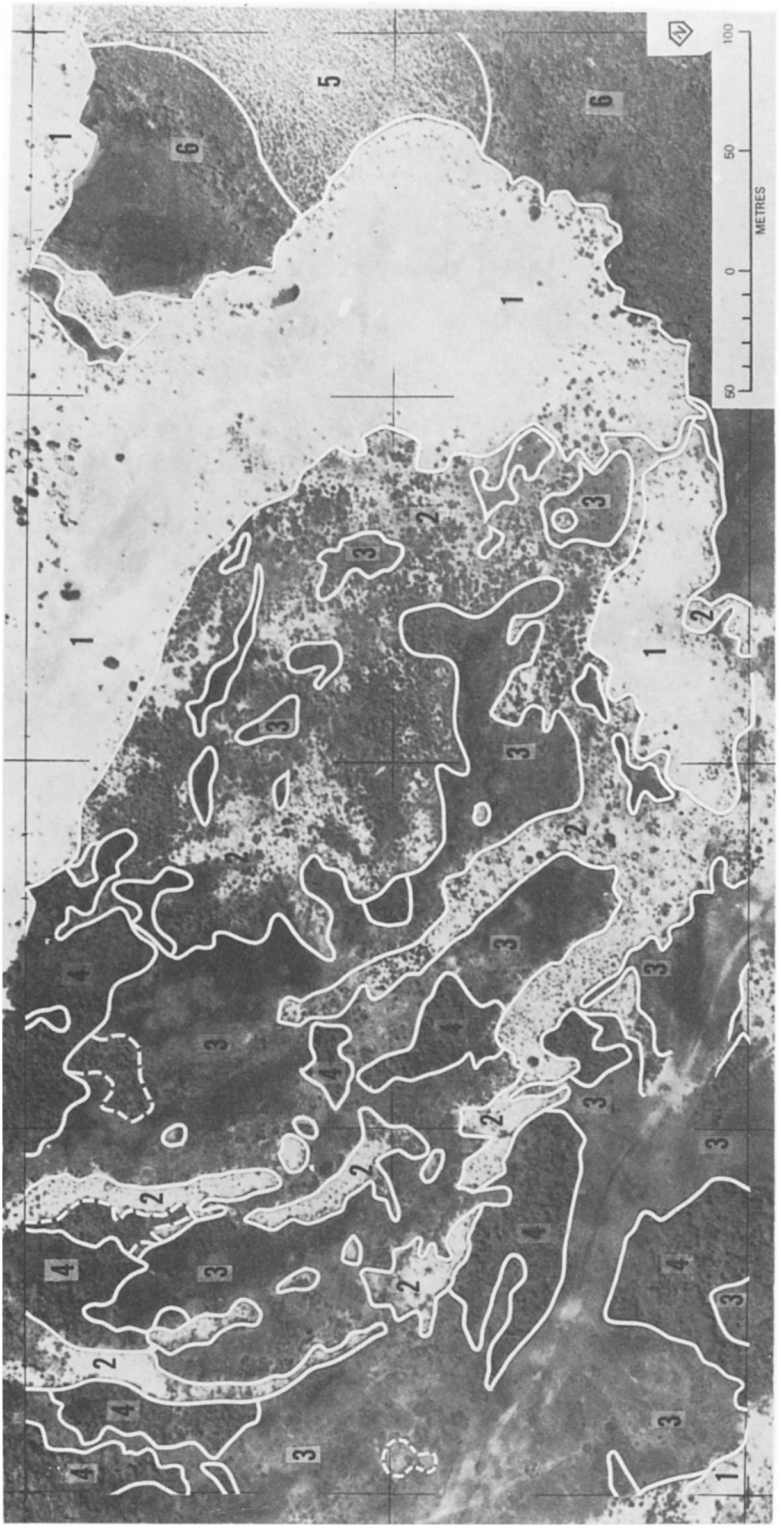


FIG. 2. Air photograph enlargement showing land elements (numbered) of the Sangujuela study plot.

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Genista sp., *Halimium halimifolium*, *Centaurium erythraea*, *Andryala* sp., *Echium* sp., *Anthemis* sp., *Loeflingia baetica*).

Element 3. Low flat areas, frequently subject to inundation at the wettest times of the year. 100% plant cover (*Panicum repens*, *Paspalum* sp., *Mentha pulegium*, *H. vulgaris*, *Illecebrum* sp., *Hypochoeris* sp., *Myosotis* sp., *C. erythraea*, *Kickxia* sp., *Senecio jacobaea*, *Tolpis barbata*, *Plantago* sp., *Hypericum perforatum*, *Lotus* sp.). All pastures occurred in this element.

Element 4. The lowest areas (about 0·5m max. lower than element 3), subject to annual inundation and remaining moist for most of the year. Black soil with high organic content and some gley. 100% plant cover, mostly of shrubs, which inhibit ground vegetation (*Erica scoparia*, *Rubus ulmifolius*, *Ulex minor*, *Daphne gnidium*, *S. jacobaea*, *Juncus acutus*).

Element 5. Low facet of El Matorral.
Element 6. High facet of El Matorral } These facets were not subdivided to elements as the area involved was very small.

Elements 2–4 comprise a single facet of more or less flat areas (relief to 1·5 m) between sand dunes formed by wind action. The length of interface between element 3, the main feeding areas for rabbits, and element 2, the main warren building areas, was 3570 m.

The distributions of warrens among land elements in the spring and autumn surveys are shown in Table 3. The total number of entrances counted was 158, amongst 41

TABLE 3. Distribution of rabbit warrens in the Sanguijuela study plot

Element	No. of warrens	No. of entrances	Proportion of entrances active Spring %	Autumn %
1	2	3	66·7	0
2	25	121	64·3	75·8
3	10	25	84·0	4
4	0	0	–	–
5	1	7	28·6	0
6	1	2	100	0

warrens. Of these, 14 were single entrances. Active entrances numbered 105 in spring (66·5%) and 22 (13·9%) in autumn. Warren size ranged from 1 to 20, mean 3·9, entrances. In autumn only two additional entrances were found. Warrens were built mainly at the junction of elements 2 and 3. Several of the warrens were in element 3 and a small number, where suitable conditions existed, in element 1. There were no warrens in element 4. It is instructive that in autumn nearly all active entrances were confined to the sandy ridges (element 2) bordering the moist flat areas (elements 3 and 4).

Bush warrens, although difficult to quantify, occurred extensively in element 4 and, to a lesser extent in element 3. Thickets of *U. minor*, *R. ulmifolius* and *J. acutus* were used for bush warrens. The thickets covered about 67% of element 4, and 97% of the thickets occurred in that element. Rabbits were seen to be living in these thickets.

Most faecal pellets (Table 4) were in element 3, the pasture element, followed by element 4, in both spring and autumn. Fewest were in elements 1 and 2. These differences and differences between seasons (spring and autumn) were highly significant. Scratches were found only in elements 2 and 5. Feeding activities were therefore concentrated in the lower and damper areas.

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TABLE 4. Relation between counts of rabbit sign, land elements and seasons in the Sanguijuela study plot

Land system and facet		Land element	Faecal[1] pellets		Scratches[1]		No. of obs. (*n*)
			S	A	S	A	
Dunas Bajas	Sand Deflation flats	1 (sand)	2·9	5·0	0·0	0·0	20
		2 (high)	29·1	68·3	0·1	0·1	20
		3 (inter-mediate)	118·7	472·0	0·0	0·0	20
		4 (low)	94·2	299·6	0·0	0·0	20
El Matorral	High	5 (high)	72·6	85·2	0·4	0·2	5
	Low	4 (low)	26·6	97·0	0·0	0·0	5
		Significance of difference between mean (analysis of variance, paired samples)					
	Between elements	$P <$	0·001	0·001	0·001	0·091	
	Between seasons	$P <$	0·001			0·349	

[1] Mean number per 3 m². S = spring, A = autumn.

El Muerto study plot

El Muerto study plot (Fig. 3) was situated entirely in Las Navas land system and included both high and low facets. The high facet included only one element (element 1) and the low facet two elements. The elements were defined by relief and vegetation, element 1 having 30–60% plant cover and element 2, 60–80% cover. Element 3 was subject to inundation in winter and generally had 100% plant cover, with grass in a few places. The identified characteristics of these elements were as follows:

Element 1. High ground, soil of highly permeable yellow sand, plants dominated by *Halimium halimifolium*, *Lavandula stoechas*, *Rosmarinus officinalis*, *Cistus* sp., *Armeria* sp., *H. commutatum* and clumps of *Corema album.*

Element 2. Slightly raised in the low facet. Sandy soil, not subject to inundation. Plant cover included *Erica umbellata*, *H. halimifolium*, *Calluna vulgaris*, and *Ulex* sp.

Element 3. Lowest areas of the low facet, which were subject to temporary winter inundation. Shrub cover dense and almost impenetrable, of *E. scoparia.* Soil of high organic content in elements 1 and 2, and pastures in a few places.

The total length of interface between elements 1 and 2 was 1380 m and between 2 and 3, 1430 m.

The total number of warren entrances counted in spring was 142 in 42 warrens, of which 14 were single entrance burrows. Many of the latter were shallow and short, suggesting that they were not breeding stops. Active entrances in spring numbered 36 (25·4%) and in autumn 1 (0·7%). Warren size ranged from 1 to 10, mean 3·4, entrances. No bush warrens were found.

Warrens (Table 5) tended strongly to be grouped on the peripheral areas of element 2, or on slightly raised ground within that element. About 25% were centrally placed in element 1. No warrens occurred in element 3. Active entrances were similarly distributed in spring.

Most faecal pellets (Table 6) were in areas of pasture (element 3), notably in the north-east corner of the plot. The pattern was similar in spring and autumn. Differences in pellet counts between elements were highly significant in both spring and autumn.

Most scratches were in element 1 (Table 6), and the greatest increase in numbers of scratches from spring to autumn occurred in element 3. Analysis of variance for scratch

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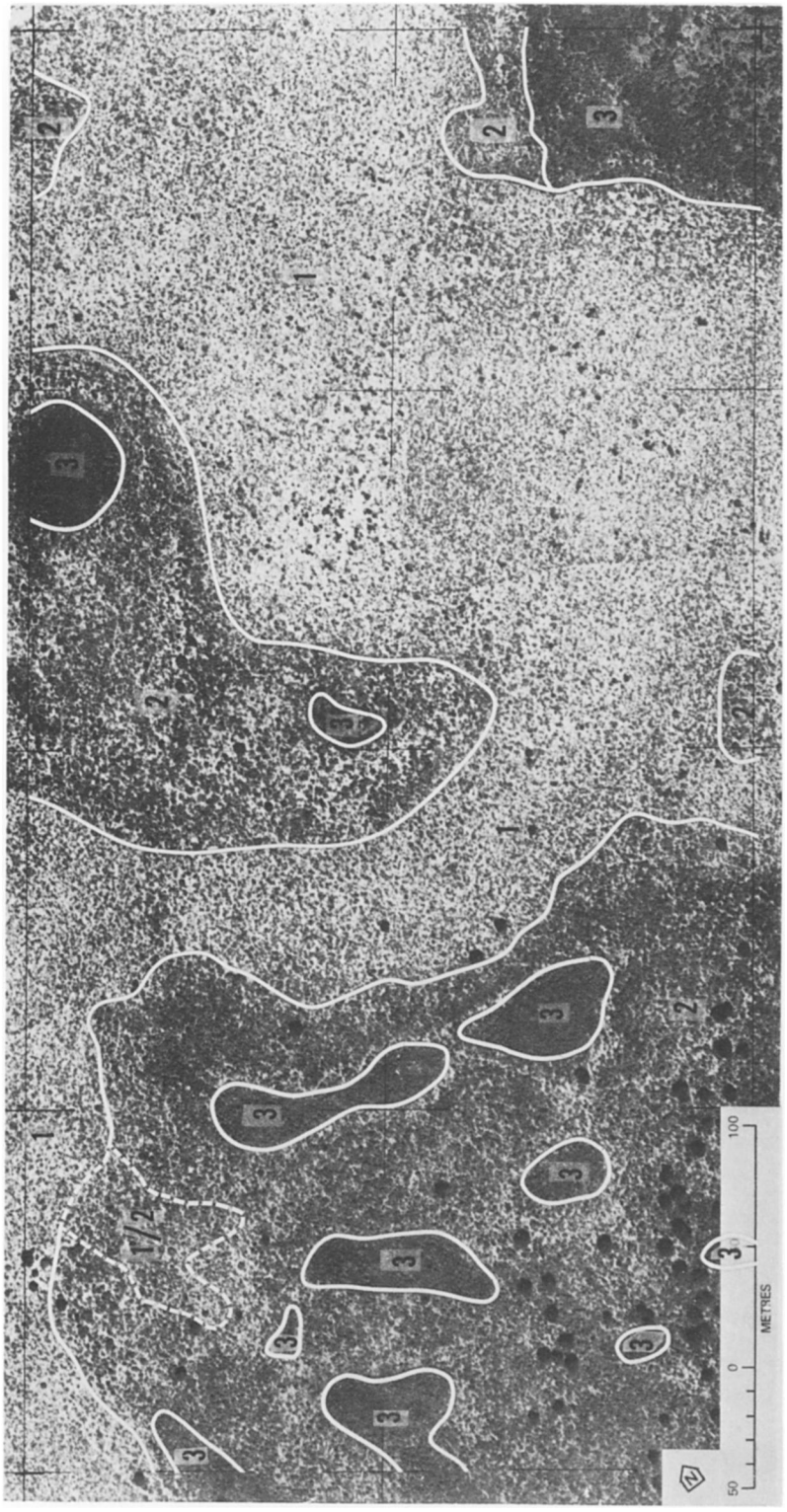


FIG. 3. Air photograph enlargement showing land elements (numbered) of El Muerto study plot.

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TABLE 5. Distribution of rabbit warrens in El Muerto study plot

Element	Warrens	Entrances	Entrances active Spring %	Entrances active Autumn %
1	24	73	13·6	0
2	18	69	33·4	1·4
3	0	0	—	—

counts revealed significant ($P < 0.002$) differences between elements in spring, but not in autumn. Overall autumn scratch densities were not significantly ($P > 0.05$) different from spring, though the tendency was for an increase in scratches in autumn in elements 1 and 3.

The data show that the main activities of the rabbit in the higher and drier land systems of the Coto Doñana are concentrated around areas sufficiently moist to provide a source of food.

TABLE 6. Relation between counts of rabbit sign, land elements and seasons in El Muerto study plot

Land system and facet		Land element	Faecal[1] pellets S	Faecal[1] pellets A	Scratches[1] S	Scratches[1] A	No. of obs. (*n*)
Las Naves	High	1 (high)	8·8	12·5	1·1	1·7	20
	Low	2 (low)	25·6	25·6	0·9	0·8	20
		3 (very low)	69·5	71·8	0·1	1·0	20
		Significance of difference between means (analysis of variance, paired samples)					
	Between elements	$P <$	0·001	0·001	0·002	0·051	
	Between seasons	$P <$		0·097		0·079	

[1] Mean number per 3 m². S = spring, A = autumn.

DISCUSSION

The data clearly demonstrate that rabbits on the study area were distributed patchily, and their pattern of distribution in relation to habitat was readily measurable on both small and large scales from observations of animals or of indices of their activities. On a small scale (land system) rabbits were more common in the moister (and grassier) parts of the coastal dune systems. The higher and drier dunes carried fewer rabbits. On a larger scale (land facets and elements) the habitat is clearly more favourable where low sandy ridges interdigitate or abut moist grasslands. The pattern of distribution of rabbits can be explained in the light of previous work (Myers 1971) as resulting from a suitable admixture of the right kind of habitat in which to dig and breed—sandy ridges, a food vital for both reproduction and survival—green herbage, and shelter from predation in both warrens and bush.

In drier Australian environments the same kind of relationship with habitat has been observed. In arid New South Wales sand dunes become an important habitat for rabbits after periods favourable for plant growth (Myers & Parker 1975b). In drought, however, rabbit populations are limited to the neighbourhood of drainage channels and swamps. So, similar ecological processes are involved. Furthermore, with high temperatures and seasonal rainfall the rabbit might be expected to respond in a similar way wherever it exists in the wild state. Its size and physiology permit little alternative.

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In Australia, Britain and elsewhere, objectives in managing rabbit populations are aimed at controlling it as a pest. Conversely, in the Coto Doñana, the rabbit is important for the survival of many wildlife species, e.g. Lynx (Delibes *et al.* 1975, Rogers 1978). Landscape analysis is appropriate to both situations. In Australia rabbits may be driven locally extinct by destruction in summer of special refuge warrens bordering swamps and streams (Myers & Parker 1975b). In the Coto Doñana rabbits depend heavily on refuge areas, the deflation flats of Las Dunas and the border of Las Marismas. Other grazing mammals compete with rabbits for the same resource (Rogers & Myers unpublished). Management of the rabbit in the Coto Doñana is thus intimately related to management of the grassy lowland areas. Our results show that further research is necessary to determine precise management practices compatible with Park policies and the needs of other species; but even without such research, sensible management decisions can still be made, such as relieving the fragile pasture areas of the pressure of grazing domestic stock.

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